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Commentary

Origins of endemic island tortoises in the western Indian Ocean: a critique of the human-translocation hypothesis

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Abstract

How do organisms arrive on isolated islands, and how do insular evolutionary radiations arise? In a recent paper, Wilmé *et al.* (2016a) argue that early Austronesians that colonized Madagascar from Southeast Asia translocated giant tortoises to islands in the western Indian Ocean. In the Mascarene Islands, moreover, the human-translocated tortoises then evolved and radiated in an endemic genus

(*Cylindraspis*). Their proposal ignores the broad, established understanding of the processes leading to the formation of native island biotas, including endemic radiations. We find Wilmé *et al.*'s suggestion poorly conceived, using a flawed methodology, and missing two critical pieces of information: the timing and the specifics of proposed translocations. In response, we here summarise arguments that could be used to defend the natural origin not only of Indian Ocean giant tortoises but also of scores of insular endemic radiations worldwide. Reinforcing a generalist's objection, the phylogenetic and ecological data on giant tortoises, and current knowledge of environmental and paleogeographical history of the Indian Ocean, make Wilmé *et al.*'s argument even more unlikely.

Keywords

Colonisation, endemic radiation, giant tortoises, islands, long-distance dispersal, transoceanic dispersal.

Introduction

Proposing original hypotheses that question current paradigms is essential in the advancement of science. However, when such alternative hypotheses overlook or misinterpret existing knowledge, they are more likely to stir unproductive controversy than contribute to our understanding of events and processes. By neglecting data and understanding from a wide range of fields (phylogenetics, evolutionary biology, ecology, geology, oceanography and environmental history), Wilmé *et al.*'s (2016a; hereafter referred to as Wilmé *et al.*) recent proposal of a possible role of human translocation to explain the presence of giant tortoises on remote islands in the western Indian Ocean (WIO) regrettably belongs in the latter category. A human-translocation (HT) hypothesis for the origin of the WIO giant tortoise radiations is no less far-fetched than it would be in explaining any one of a plethora of similar insular endemic radiations worldwide, be they volant (e.g., Hawaiian honeycreepers, Darwin's finches) or non-volant (e.g., *Anolis* lizards, *Phelsuma* geckos).
Here we present and discuss several lines of critique, any one of which represents a major obstacle to the proposal by Wilmé *et al*., as well as to any similarly unfounded future HT-hypotheses.

Methodological flaws

As the key evidence for their hypothesis, Wilmé *et al.* state that their "evaluation is based on an analysis of more than 700 peer-reviewed publications from several pertinent fields". The appendix referred to indeed contains a list of 700 papers, but aside from a single thematic keyword assigned to each, no further details are given, revealing severe shortcomings in the method used. Firstly, and contrary to the authors' claim, nowhere in the paper or appendices is an actual analysis based on these 700 papers to be found. Secondly, there are no search- and/or inclusion criteria for the 700 papers listed. Thirdly, a specific list of lines of arguments or data from these 700 papers, clearly stating supporting and contradicting information, is notably absent. This third point is of special interest to several of the authors of this response. Many of our papers are on that list, and our data and results do not support Wilmé *et al.*'s hypothesis.

Equally problematically, Wilmé *et al.*'s HT-hypothesis is not always explicit about exactly what is being proposed in terms of which tortoise taxa were moved when, from Madagascar to the "small islands in the SWIO". It is likewise unclear when their arguments are concerned only with the Mascarenes, and when they also include Aldabra Atoll, the only other small island mentioned. In either case, several important islands and archipelagos that also harboured giant tortoises are not mentioned at all, e.g., the granitic Seychelles and several of the outer Seychelles islands.

Finally, in what is perhaps the clearest formulation of the key postulate of their hypothesis, Wilmé *et al.* state: "[t]he land tortoises found on the small islands in the [south-western Indian Ocean] could have been translocated from Madagascar by Austronesian sailors". The reference cited is another recent paper by the same authors (Wilmé *et al.*, 2016b), which hypothesizes that early Austronesians used sea turtles as navigation aids, but which contains no mention of Austronesian translocations of tortoises from Madagascar to small islands in the WIO. This circular logic serves well as an overall example of the flawed arguments supporting their hypothesis.

Island tortoises and the Indian Ocean radiations

Humans (in particular sailors in historic times) have indeed been known to move tortoises between islands (Rhodin *et al.* 2015). When an island population is little diverged from populations elsewhere, and when supported by historical and genetic evidence, a hypothesis of an HT origin may be reasonable. An excellent example of the substantial weight of evidence required to support such a hypothesis is provided by recent, detailed molecular data from the Galápagos giant tortoises, *Chelonoidis* spp., which suggest that some tortoises could have been moved between islands in the archipelago by humans in the last few hundred years (e.g., Rusello *et al.*, 2007; Poulakakis *et al.*, 2008, 2012). Perhaps more important than the absence of such supporting evidence provided by Wilmé *et al*., we must emphasise that there is an enormous difference between proposing an HT-origin for populations little-diverged from the proposed source population, as in the case above, and proposing such an origin for taxa that have been described as an insular radiation with single-island endemics, as is the case here. The Indian Ocean tortoises considered in Wilmé *et al.*'s hypothesis belong to two genera. The first, *Cylindraspis*, contained five species (all now extinct), each endemic to a single island in the Mascarenes, and genetic analyses have found that mean pairwise genetic divergence between these species ranged from 2 to 17% in mtDNA (Austin & Arnold, 2001). The second, *Aldabrachelys*, contained at least three species; two sympatric species on Madagascar that went extinct ~1000 years ago and one species found across many islands to the north, including Aldabra and the Seychelles. Wilmé *et al.* do concede that the significant morphological and genetic divergence between the two endemic giant tortoise genera in the WIO represents a “possible contradiction” to their hypothesis, but nevertheless then unexplainably disregard this evidence. Contrary to Wilmé *et al.*, who imply that the biogeographic origins of the two genera are not supported by phylogenetic inference, we and others (Austin & Arnold, 2001; Le *et al.*, 2006) have shown that *Aldabrachelys* and *Cylindraspis* form part of a wider clade of Indian Ocean tortoises that includes the Madagascan genera *Astrochelys* and *Pyxis*. Area cladograms suggest that all Indian Ocean island tortoises derive from a single colonization of the WIO (Le *et al.*, 2006). Even if we were to collapse nodes gaining less than 100% branch support (increasing the potential number of colonization events), the data imply numerous *in situ* speciation events. If Wilmé *et al.*’s suggestion that the observed morphological and molecular evolution occurred *in situ* after human translocation sometime in the last 4,000 years were true, then this would require a mtDNA evolutionary rate *at least* 2–3 orders of magnitude faster than the "standard" vertebrate lineage rate of 1x10-8 substitutions/site/yr. Such accelerated rates have never been observed over the time scales that Wilmé *et al.* suggest (Molak & Ho, 2015).

Morphologically, it seems perplexing that the Mascarene *Cylindraspis* tortoises would have changed so much, so rapidly after being translocated by Austronesians from Madagascar to these islands, while *Aldabrachelys gigantea* did not change after Austronesians moved it to Aldabra (morphologically, *A. gigantea* is very similar to the extinct *A. abrupta* from Madagascar). Unfortunately, Wilmé *et al*. provide no explanation for this great difference.

Indian Ocean biogeography and phylogeography

Wilmé *et al.*’s argument centres on a perceived infinitesimal probability of giant tortoises colonizing small, “young” oceanic islands via passive floating or swimming against prevailing ocean surface currents. Aldabra Atoll is among the very youngest and smallest of all WIO islands known to have harboured giant tortoises. It has been colonized by giant tortoises following each of the three times it re-emerged during the sea level fluctuations of the last 320,000 years (Taylor *et al.*, 1979), thus singlehandedly refuting Wilmé *et al.*’s argument about probability. Even if we were to accept that the origin of the current population of Aldabra tortoises was Austronesian translocation from

Madagascar to Aldabra in the last few thousand years, this still does not explain how the tortoises arrived on the previous two 'incarnations' of Aldabra in the last 320,000 years.

The WIO of the last 40 MY years was a rich tapestry of appearing and disappearing islands, of growing and shrinking islands, from very small to very large. At the scale of the entire WIO, while the current Mascarene Islands are indeed small (and Reunion is unambiguously young), bathymetry, geology and sea-level reconstructions reveal that the Mascarene Bank to the north represented a larger and much older (up to 40 My), set of large, flat islands that are mostly now submerged. These formed a series of potential stepping stones separated by much shorter distances and would have provided a natural link to the granitic Seychelles and Madagascar (Cheke & Hume 2008; Warren *et al.* 2010).

Especially during the last 1 million years when sea level fluctuations were maximized due to astronomical forcing, both the connectivity and areas of islands were increased substantially during glacial times that encompassed 90% of this period (Fig. 1). The former presence of numerous source populations of giant tortoises on such islands therefore seems likely. Moreover, during the LGM the massive banks were islands above sea level, and would to a large extent have blocked or at least weakened the south-westward effect of the SWIO gyre. During this time, the north-westerly flowing trade winds would likely have been more influential than the gyres, and subdecadal cyclonic storms would also greatly have enhanced connectivity and random dispersal in all directions (De Boer 2014). Lastly, while presently predominant sea surface currents do flow east to west, large transient gyres and countercurrents are a regular occurrence and can last several months, showing that ocean currents can and do flow in a direction favourable for west-to-east dispersal from Madagascar or the Seychelles to the Mascarenes (Video S1).

For a broad range of major taxa, including flightless groups such as reptiles, phylogenetic evidence demonstrates that the closest relatives of Indian Ocean forms occur in Asia, not Africa. Furthermore, estimated divergence times post-date Gondwanan fragmentation by a considerable margin. Together these results suggest that colonization of the WIO from Asia (or the reverse) by flightless terrestrial species has occurred repeatedly (Warren *et al.*, 2010). In fact, drifting on oceanic currents is likely an important contributor to oceanic island biotas worldwide. Even for the Hawaiian archipelago – among the most remote archipelagos on the globe – a recent review posits oceanic drift as the most likely mode of immigration for at least eight lineages (Gillespie *et al.*, 2012). Islands worldwide show that colonization events arising from passive drift, given enough time, are not only probable but extremely likely.

Moreover, phylogenetic data show that once a lineage colonized one island in a WIO archipelago through long-distance dispersal, subsequent inter-island colonization events were very frequent across a wide range of terrestrial organisms. These include many non-volant animals, such as skinks and flightless crickets (Austin *et al*., 2009; Warren *et al*., 2016), and a long list of vertebrate-dispersed plants, often with large seeds, including species from the families of Monimiaceae and Arecaceae (Renner *et al*., 2010; Baker & Couvreur 2013). It is unclear to us why tortoises should be so uniquely unlikely to have colonized the WIO islands on their own, compared to these taxa.

Early Austronesians in the WIO and archaeological and paleoecological evidence

Exactly when could Austronesians have translocated tortoises? This is never clearly stated by Wilmé *et al*., but there are several key sections that suggest speculative inferences. For example, the authors refer to the timing of "[h]umans first colonized Madagascar 4000 years ago", even though this date refers to coastal archaeological sites with evidence of hunter-gatherer foraging by unidentified people, rather than to evidence of actual colonization or settlement by Austronesians (Dewar *et al*. 2013). Wilmé *et al*. then continue with the very next sentence stating that "people have been making transoceanic journeys since 45,000 years bp". Are we here supposed to make the logical inference that Madagascar could have been visited and perhaps colonized by Austronesians up to 45,000 years ago? If not, why is this information given here? Moreover, the source they cite for such early transoceanic journeys, Balter (2007), is 1) a news article that reports partly controversial studies presented at a conference about the earliest origins of human seafarers, and 2) concerns early humans in Southeast Asia crossing gaps of up to a few hundred km between islands – hardly qualifying as 'transoceanic journeys' in comparison to the proposed journey across the entire Indian Ocean (a distance of thousands of km).

Wilmé *et al.* argue that sea level rises could have erased any evidence of early Austronesians in the Mascarenes. This appears to be an argument of convenience, and we cannot think of any mechanism by which an early Austronesian presence in these islands would have been restricted to coastal areas. Areas currently well above sea level would have been just as hospitable to humans and their commensal species. Worldwide, any island with a significant period of pre-European settlement has experienced contractions and extinctions of its native flora and fauna (Burney & Flannery, 2005). Had Austronesians been present on the Mascarene Islands, there should be plentiful evidence of pre-European extinction waves and introductions of commensal and other exotic species (including pests). No such evidence has yet been found, while the post-European extinction wave is among the most dramatic worldwide, with the documented extinction of 50–60% of the native land vertebrate fauna (Cheke & Hume, 2008), and the extirpation and extinction of dozens of plant species in Mauritius, in particular palms (de Boer, 2014).

On the contrary, there is a ubiquitous presence of dung-fungus spores – indicating the presence of large herbivorous vertebrates – in the lowlands of the Mascarenes reaching back thousands of years (e.g., de Boer *et al.*, 2015), and abundant evidence of the pre-European presence of giant tortoises in the Mascarenes from fossil bones (Rijsdijk *et al.*, 2015).

Giant tortoises are excellent oceanic dispersers and island colonizers

We believe that the above arguments are sufficient to reject Wilmé *et al.*'s proposal. However, emerging ecological knowledge of Aldabra giant tortoises in their native habitat can serve as a final nail in the coffin. Wilmé *et al.* emphasise the Aldabra giant tortoise as a "non-swimming" animal that would have "drifted passively" between islands, and question whether "physiologically stressed individuals who have been afloat for extended periods without any food intake" can reproduce.

Giant tortoises are indeed excellent drifters as they are positively buoyant, and do not need to expend much energy to stay alive in water. However, Aldabra tortoises *can* also swim actively, as can be frequently observed on Aldabra Atoll. Moving alongside a tortoise swimming across a pond, one has to move at a walking pace to keep up with the animal (Video S2). The tortoises also frequently cross to or from favoured browsing areas in the mangroves during the outgoing and incoming tide, respectively; sometimes against tidal waters rushing out or in (Fig. 2a). Such activities carry the risk of being carried away by the tide and swept out to sea. Indeed, during the last few years, scientists and staff from the Seychelles Islands Foundation's research station on Aldabra have spotted tortoises adrift in the open ocean outside the reef in various places around the atoll (Fig. 2b). Once adrift, these tortoises can survive for several months, as was demonstrated by an Aldabra tortoise found alive on the Tanzanian coast, covered in barnacles (Gerlach *et al.*, 2006). Such events are likely to happen much more frequently than recorded. For example, in the 1980s two Aldabra tortoises, likewise covered in barnacles, were found alive on the coast of Kenya and brought to the Haller Park, where they entered the breeding herd (R. Haller, pers. comm.). On Aldabra, long-term GPS data is revealing that the tortoises can walk several kilometres within a week, with significant amounts of time spent moving non-stop (RB & DMH, unpubl. data). Given how much easier it is to move in water, it is clear that a giant tortoise drifting in the ocean would be capable of sustained directional swimming towards any island appearing on the horizon.

Regarding tortoises as island colonizers, our interpretation of facts is thus contrary to Wilmé *et al*.'s interpretation of largely the same facts. Tortoises can survive long periods of being adrift in the ocean without food and water, and females can store sperm for several years (Pearse *et al.* 2001). Even if we disregard the ability of tortoises to swim actively, these facts translate into giant tortoises showing all the characteristics of proficient long-distance dispersers being able to easily cross large ocean barriers, and thus being among the most *likely* tetrapods to reach and colonize isolated oceanic islands.

Conclusion

Wilmé *et al.*'s HT-hypothesis goes against substantial ecological, evolutionary, and biogeographical evidence, and the HT-hypothesis for the endemic Indian Ocean tortoise radiations can be safely ruled out. Worryingly, their hypothesis also presents a potential hindrance to conservation and education. The Indian Ocean islands are a hotspot of unique biological diversity. This diversity has experienced some of the highest levels of extinction worldwide and continues to be under threat from human activities. Throughout the region, conservation biologists and teachers work hard to communicate to the general public and politicians the importance of preserving this heritage, and distinguishing the unique diversity (the native biota) from the non-unique and often ecologically detrimental diversity (elements of the biota that are introduced and often invasive). A paper such as Wilmé *et al.* is a potential spanner in the works, blurring this important distinction with an argument that has no foundation.

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References

Austin, J., Arnold, E. & Jones, C. (2009) Interrelationships and history of the slit-eared skinks (*Gongylomorphus*, Scincidae) of the Mascarene islands, based on mitochondrial DNA and nuclear gene sequences. *Zootaxa*, **2153**, 55-68.

Austin, J.J. & Arnold, E.N. (2001) Ancient mitochondrial DNA and morphology elucidate an extinct island radiation of Indian Ocean giant tortoises (*Cylindraspis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 2515-2523.

Baker, W.J. & Couvreur, T.L. (2013) Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography*, **40**, 274-285.

Balter, M. (2007) In search of the world's most ancient mariners. *Science*, **318**, 388-389.

Burney, D.A. & Flannery, T.F. (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends In Ecology & Evolution*, **20**, 395-401.

Cheke, A.S. & Hume, J.P. (2008) *Lost land of the dodo*. Christopher Helm, London, UK.

de Boer, E.J. (2014) *Mauritius since the last ice age: paleoecology and climate of an oceanic island*. PhD Thesis, University of Amsterdam, The Netherlands.

de Boer, E.J., Vélez, M.I., Rijsdijk, K.F., de Louw, P.G., Vernimmen, T.J., Visser, P.M., Tjallingii, R. & Hooghiemstra, H. (2015) A deadly cocktail: How a drought around 4200 cal. yr BP caused mass mortality events at the infamous 'dodo swamp'in Mauritius. *The Holocene*, 0959683614567886.

Dewar, R.E., Radimilahy, C., Wright, H.T., Jacobs, Z., Kelly, G.O. & Berna, F. (2013) Stone tools and foraging in northern Madagascar challenge Holocene extinction models. *Proceedings of the National Academy of Sciences USA*, **110**, 12583-12588.

Gerlach, J., Muir, C. & Richmond, M.D. (2006) The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History*, **40**, 2403-2408.

Gillespie, R.G., Baldwin, B.G., Waters, J.M., Fraser, C.I., Nikula, R. & Roderick, G.K. (2012) Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology & Evolution*, **27**, 47-56.

Le, M., Raxworthy, C.J., McCord, W.P. & Mertz, L. (2006) A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. *Molecular Phylogenetics And Evolution*, **40**, 517-531.

Molak, M. & Ho, S.Y. (2015) Prolonged decay of molecular rate estimates for metazoan mitochondrial DNA. *PeerJ*, **3**, e821.

Pearse, D. & Avise, J. (2001) Turtle mating systems: behavior, sperm storage, and genetic paternity. *Journal of Heredity*, **92**, 206-211.

Poulakakis, N., Russello, M., Geist, D. & Caccone, A. (2012) Unravelling the peculiarities of island life: vicariance, dispersal and the diversification of the extinct and extant giant Galapagos tortoises. *Molecular Ecology*, **21**, 160 - 173.

Poulakakis, N., Glaberman, S., Russello, M., Beheregaray, L.B., Ciofi, C., Powell, J.R. & Caccone, A. (2008) Historical DNA analysis reveals living descendants of an extinct species of Galapagos tortoise. *Proceedings of the National Academy of Sciences*, **105**, 15464–15469.

Renner, S.S., Strijk, J.S., Strasberg, D. & Thébaud, C. (2010) Biogeography of the Monimiaceae (Laurales): a role for East Gondwana and long-distance dispersal, but not West Gondwana. *Journal of Biogeography*, **37**, 1227-1238.

Rhodin, A., Thomson, S., Georgalis, G., Karl, H., Danilov, I., Takahashi, A., de la Fuente, M., Bourque, J., Delfino, M. & Bour, R. (2015) Turtles and tortoises of the world during the rise and global spread of humanity: First checklist and review of extinct Pleistocene and Holocene chelonians. *Chelonian Research Monographs*, **5**, 1-66.

Rijsdijk, K. F., Hengl, T., Norder, S. J., Otto, R., Emerson, B. C., Ávila, S. P., López, H., van Loon, E. E., Tjørve, E., & Fernández-Palacios, J. M. (2014). Quantifying surface-area changes of volcanic islands driven by Pleistocene sea-level cycles: biogeographical implications for the Macaronesian archipelagos. *Journal of Biogeography* **41**, 1242–1254.

Rijsdijk, K.F., Hume, J.P., De Louw, P.G.B., Meijer, H.J.M., Janoo, A., De Boer, E.J., Steel, L., De Vos, J., Van Der Sluis, L.G., Hooghiemstra, H., Florens, F.V.B., Baider, C., Vernimmen, T.J.J., Baas, P., Van Heteren, A.H., Rupaer, V., Beebeejaun, G., Grihault, A., Van Der Plicht, J., Besselink, M, Lubeek, J.K., Jansen, M., Kluiving, S.J., Hollund, H., Shapiro, B., Collins, M., Buckley, M., Jayasena, R.M., Porch, N., Floore, R., Biedlingmaier, A., Leavitt, J., Monfette, G., Kimelblatt, A., Randall, A., and Claessens, L.P.A.M. (2015) A review of the dodo and its ecosystem: Interdisciplinary research of a vertebrate concentration Lagerstätte in Mauritius. pp. 3-20 in Claessens L.P.A.M., Meijer, H.J.M., Hume, J.P, & Rijsdijk, K.F. (eds.), Anatomy of the Dodo (*Raphus cucullatus* L., 1758): An osteological study of the Thirioux specimens. Society of Vertebrate Paleontology Memoir 15*. Journal of Vertebrate Paleontology*, **35**:3-20 (Supplement 1).

Russello, M.A., Beheregaray, L.B., Gibbs, J.P., Fritts, T., Havill, N., Powell, J.R. & Caccone, A. (2007) Lonesome George is not alone among Galápagos tortoises. *Current Biology*, **17**, 317-318.

Taylor, J.D., Braithwaite, C.J.R., Peake, J.F. & Arnold, E.N. (1979) Terrestrial faunas and habitats of Aldabra during the late Pleistocene. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **286**, 47-66.

Warren, B.H., Strasberg, D., Bruggemann, J.H., Prys-Jones, R.P. & Thébaud, C. (2010) Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics*, **26**, 526-538.

Warren, B.H., Baudin, R., Franck, A., Hugel, S. & Strasberg, D. (2016) Predicting where a radiation will occur: Acoustic and molecular surveys reveal overlooked diversity in Indian Ocean Island crickets (Mogoplistinae: *Ornebius*). *PloS one*, **11**, e0148971.

Wilmé, L., Waeber, P.O. & Ganzhorn, J.U. (2016a) Human translocation as an alternative hypothesis to explain the presence of giant tortoises on remote islands in the south-western Indian Ocean. *Journal of Biogeography*.

Wilmé, L., Waeber, P.O. & Ganzhorn, J.U. (2016b) Marine turtles used to assist Austronesian sailors reaching new islands. *Comptes rendus biologies*, **339**, 78-82.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1 Surface current dynamics in the Indian Ocean 2007–2008.
not uploaded to ManuscriptCentral – mp4 file can be found/viewed here [19.2 mb]:
https://www.dropbox.com/s/hfrm6zv0rria29f/Hansen%20et%20al.%20Video%20S1.mp4?dl=0

Video S2 Aldabra giant tortoise, *Aldabrachelys gigantea*, swimming across a pond on Aldabra Atoll, Seychelles.
not uploaded to ManuscriptCentral – mp4 file can be found/viewed here [21.7 mb]:
https://www.dropbox.com/s/4ppn2suz438ev2s/Hansen%20et%20al.%20Video%20S2.mp4?dl=0

Appendix S1 Additional methodological information for Fig. 1 and Video S1.

Figure legends

Figure 1. Islands in the western Indian Ocean region today, compared to the situation during the Last Glacial Maximum (LGM; ±20 kyr BP), when sea levels were 120 m below the current level. The current extent of islands is shown in dark brown, the extent of islands during the LGM is shown in light orange. The numbers between brackets represent the area (km^2) of the island, or of the largest island in an archipelago, during the LGM (detailed methodology in Rijsdijk *et al.* 2014).

Figure 2. Giant Aldabra tortoises (*Aldabrachelys gigantea*) on Aldabra Atoll, Seychelles. (a) Tortoise crossing between mangrove areas during incoming tide, La Gigi area, Picard. (b) Tortoise found afloat in open ocean outside one of the channels between Picard and Grand Terre (photo credits: (a) Dennis Hansen, (b) Lotte Reiter).